INFLUENCE OF COLLECTIVE FEEDING ON WEIGHT GAIN AND SIZE VARIABILITY OF ANELOSimus JABAQUARA LEVI 1956 (ARANeAE: THERIDIIDAE)

by

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Summary

Differences in the size and weight of spiders within colonies may be an important factor for determining dispersion and food distribution among nestmates. In this study we report on the variation in size of spiders from 27 colonies of \textit{A. jabaquara}, collected during one year. We also conducted an experiment under laboratory conditions to test if prey size, and consequently, collective or individual capture behaviours, influence the establishment of weight differences. Female size variation within colonies was high, increasing slightly from March to September. However, from November to January the variation was much lower, probably as a consequence of the emigration of large spiders during the reproductive period. Spiders that fed on large flies in the laboratory experiment grew more and collective feeding seemed to induce a larger variation in weight among individuals. These results indicate that collective feeding promotes an unequal distribution of food in \textit{A. jabaquara} colonies.

Keywords: \textit{Anelosimus jabaquara}, social spiders, collective feeding, size variability, prey capture behaviour.

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Introduction

The unequal distribution of food promoted by dominance hierarchies is very common in social carnivore groups (e.g. Tilson & Hamilton, 1984; Frank, 1986; Gese et al., 1996). Generally, when large prey items are captured cooperatively, low-ranking individuals have to wait for the initial exploitation of the acquired resources by members of the group positioned in a higher level of the hierarchy. As an alternative foraging strategy, smaller and less competitive individuals can spend more time hunting for small prey, which can be captured and consumed without the participation of others (Gese et al., 1996; Ebert, 1998).

Another interesting aspect involved in food distribution is that some individuals can use the investment of others in prey capture, arriving at the capture site after prey immobilisation (Barnard & Sibly, 1981; Vollrath & Rohde-Arndt, 1983; Packer & Ruttan, 1988; Ranta et al., 1996; Ebert, 1998). Acting like this, individuals can avoid energy expense and risk of injury related to prey capture (see Willey & Jackson, 1993; Rita et al., 1997).

The exploitation of other individuals’ efforts and the competitive interactions during feeding events are well described for a few species of social spiders (e.g. Vollrath & Rohde-Arndt, 1983; Whitehouse & Lubin, 1999). In Anelosimus eximius, for example, large females gain access to food by joining feeding companies or chasing smaller spiders away after the capture of a large prey. Small females are more successful at capturing small insects than large insects. Small insects can be consumed without attracting the attention of competitors (Ebert, 1998). Variation in spider size and, consequently, in the ability to obtain resources, is so important in these colonies that only competitively superior and well-fed females produce eggs. In A. jabaquara large females lay larger clutches and always emigrate from natal colonies, while small spiders often avoid the cost of new colony foundation reproducing in their original nests (Gonzaga & Vasconcellos-Neto, 2001).

But colonies of these Anelosimus species are different in some important aspects. In A. eximius, colonies collected during any period of the year are composed of individuals in many stages of development (Souza, 1995; Avilés, 1997). On the other hand, A. jabaquara colonies are always composed of individuals in the same instar or differing by only one molt (except, of course, during the period of overlapping between maternal and filial generations) (Marques et al., 1998). In addition, large A. jabaquara individuals
do not avoid involvement in prey capture (Gonzaga & Vasconcellos-Neto, 2002), as described for A. eximius (Ebert, 1998).

Gonzaga & Vasconcellos-Neto (2002) described the interactions of A. jabaquara nestmates during collective prey-capture and feeding events. After the immobilisation of a large prey, many spiders that did not participate in the capture process are attracted to the consumption site. In small laboratory groups all spiders had access to the most profitable parts of the prey, but it is possible that competition in large groups during collective feeding promotes an asymmetrical distribution of food also in this species and, consequently, an increase in size variation among nestmates.

In this study we investigated spider size variation within natural colonies during one year and the effect of prey size on the establishment of this variation. We expected collective consumption to lead to higher differences in spider size and a continuous increase in this variation during spider development.

Material and methods

Spiders size variation within natural colonies

To verify size variation during spider development, we collected four colonies at bimonthly intervals from September 1997 to July 1998, and four additional colonies in January 1999. All colonies were collected from a population located in Serra do Japi, a subtropical humid forest in Jundiaí (23°11'S, 46°52'W), state of São Paulo, Brazil. This study involved a total of 27 colonies (one web, collected in March 1998, was lost during transportation) and 2394 individuals. Colonies were randomly chosen among previously marked webs, from which we had collected and identified one adult specimen.

Carapace area was chosen as the measure of body size because it is probably less prone to short-term variations, caused by recent feeding events or temporary periods of starvation, than body weight or abdomen size. We measured carapace width and length to the nearest 0.01 mm, using a dissecting microscope with an ocular micrometer. Because carapace shape is close to rectangular, we estimated the area by multiplying width by length.

To analyse size variability within colonies we used the coefficient of variation (CV) because it is a relative measure, independent of differences in mean value (see Lewontin, 1966; Sokal & Braumann, 1980; Mcardle et al., 1990). Thus, colonies composed exclusively of adults could be compared with those composed by juveniles, with body sizes several times smaller in average.

Homogeneity of the coefficients of variation of colonies collected in each period of the year was tested using the procedure proposed by Feltz & Miller (1996). If the null hypothesis of equal populations’ coefficients of variation is not rejected, using this test, then \( V_p \) is the best estimate of CV common to all sampled populations (Zar, 1999). Where:
\[ V_p = \frac{k}{n} \sum_{i=1}^{k} v_i / \sum_{i=1}^{k} v_i; \]

\[ v_i = n_i - 1 \text{ and } V = \text{Coefficient of variation, } k = \text{number of populations (colonies)}. \]

**Laboratory experiment**

We moved one large colony to the laboratory in October 1998 and weighed all the spiders. These individuals were used to establish two experimental groups, each one composed of 3 subgroups with 9 females each. Only spiders with similar weights were used and we randomly selected the spiders to form each sub-group. They were maintained in plastic cylindrical cages (300 ml) containing twisted wire to supply web attachment sites. Each group received a different prey type treatment: relatively large flies (*Anastrepha* sp.) for group 1 (subgroups A, B and C) and small flies (*Drosophila melanogaster*) for group 2 (subgroups D, E and F). These insects were chosen because we observed that very small prey items, such as *D. melanogaster* (mean ± SD = 0.957 ± 0.156 mg, \( N = 20 \)), are often captured and consumed by single spiders. Conversely, the capture of *Anastrepha* sp. generally involved more than one spider and the consumption is always collective. Rypstra (1993) compared the proportion of biomass removed by groups of *A. eximius* from *D. melanogaster* and *Musca domestica* bodies and found similar values for both prey species. Because *Anastrepha* sp. has approximately the same weight (mean ± SD = 9.547 ± 1.894 mg, \( N = 20 \)) and body shape as *M. domestica*, we considered it appropriate for this experiment. In both treatments the available biomass for each sub-group was the same, \( \approx 50.0 \text{ mg} \) every other day. We terminated the experiment after 20 days and weighed all the spiders again.

We compared the spiders’ mean weight before and after the experiment, within subgroups, using \( t \)-tests for dependent samples. To test differences in spider weight, between groups, we considered subgroups as sample units. We performed paired \( t \)-tests using the mean values from the three subgroups before and after the experimental period. To test for differences in the coefficient of variation of spiders’ weight before and after the experiment, within each subgroup, we used a procedure developed by Miller (1991) that allows testing the difference between two coefficients of variation, assuming that data are from normal distributions. The homogeneity of variances was checked using Levene’s test (see Milliken & Johnson, 1984) and data normality using Shapiro-Wilks’ W test (Shapiro & Wilk, 1965).

**Results**

**Spider size variation within natural colonies**

Tests for homogeneity of CVs were significant for March (\( D’AD = 19.89, p < 0.001 \)), September (\( D’AD = 10.82, p < 0.025 \)) and November (\( D’AD = 9.59, p < 0.025 \)) samples, indicating that at least one CV value differed from the others in each one of these months. Conversely, the results for January (\( D’AD = 2.97, p > 0.75 \)), May (\( D’AD = 6.69, p > 0.05 \)) and July (\( D’AD = 3.41, p > 0.25 \)) indicated similarity among CVs. As such,
we calculated values of $V_p$ only for these homogeneous samples: January $V_p = 0.068$, May $V_p = 0.181$, and July $V_p = 0.209$. For the remaining months we presented only the median values (Fig. 1).

In spite of the heterogeneity of CVs in the three sample periods, it seems that variation in spider carapace area is relatively stable from spiderlings to subadults. The variation showed only a slight, but nonsignificant increase from March to September ($R^2 = 0.05$, $N = 15$, $p = 0.4$). At this point, about two months before the beginning of the reproductive period, the frequency distribution of spider carapace area is bimodal for some colonies and some individuals are much larger than others (Fig. 2). This variation decreased in November, reaching the lowest values in January.

**Laboratory experiment**

Mean body weight increased in all subgroups (Fig. 3). Before the beginning of the experiment, spider weights between groups were not statistically different ($t = 0.647$, df = 4, $p = 0.55$). After the experiment, however, spiders that fed on large flies (group 1) were significantly heavier than those that fed on small flies (group 2) ($t = 8.80$, df = 4, $p < 0.001$). In group 1,
the three subgroups had an increase in the coefficient of variation of spider weight, while in group 2 the tendency was inverse (Fig. 4). In spite of this, the tests for differences in CVs were significant only for subgroups C and E.

In subgroup C, one of two spiders that had an especially large weight increase was seen feeding on another spider. Mortality in this experiment was restricted to this cannibalistic event and to two other deaths, also in subgroup C.

**Discussion**

*Spiders size variation within natural colonies*

Our results showed that, even a short time after hatching (and probably at the same instar), some spiders have a carapace area more than three times larger than others. This large variation can be explained, in part, by the fact that
Fig. 3. Spider weight (mean ± SD) before (0) and after (1) the period in which each group received a different prey type: large flies (Anastrepha sp.) for group 1 (subgroups A, B and C) and small flies (Drosophila melanogaster) for group 2 (subgroups D, E and F). Results of t-test for dependent samples are the following: A: (t = 6.311, df = 8, p < 0.001), B: (t = 7.358, df = 8, p < 0.001), C: (t = 3.742, df = 5, p = 0.013), D: (t = 8.939, df = 7, p < 0.001), E: (t = 10.023, df = 8, p < 0.001) and F: (t = 6.110, df = 7, p < 0.001).

Fig. 4. Comparison of coefficients of variation of spider weight in each subgroup (letters) before and after the experimental period. Differences were significative only for subgroups C, in group 1, and for subgroup E, in group 2. Results of test for differences in CVs of two samples are the following: A: z = 1.096, p > 0.05; B: z = 1.337, p > 0.05; C: z = 2.350, p < 0.05; D: z = 1.405, p > 0.05; E: z = 1.982, p < 0.05 and F: z = 0.360, p > 0.05.
these spiders were born from egg sacs laid by many females and individual investment in egg size can vary according to females’ size (Gonzaga & Vasconcellos-Neto, 2001).

However, the emigration of large females before and during the reproductive period (see Gonzaga & Vasconcellos-Neto, 2001) contributes to the reduction of adult size variability in colonies. This is probably the main factor explaining why coefficients of variation of spiders’ carapace area decreased in such an accentuated manner in November and especially in January.

If the size of spiders that remain in their natal colonies is relatively homogeneous, what else could be related to high spiderling variation? Ebert (1998) found no correlation between cephalothorax width and abdomen size of a large sample of A. eximius females. This means that even spiders with approximately the same cephalothorax dimensions could present significant differences in abdomen distension (food reserves used for egg production). In addition, there is the natural variation within the egg sac and, perhaps, cannibalistic interactions, as additional factors promoting size asymmetry in the first instars.

These differences could be maintained and even increased during development due to differential metabolic rates and food extraction capabilities, competition over medium and large size prey items, energy expenses and, as proposed by Rypstra (1993), stochastic successful feeding events.

Size asymmetry among nestmates can also be related to nest size variation. Ward (1986) showed that variance in spider size, in Stegodyphus mimosarum, is significantly larger in smaller than in larger nests. According to this author, this is due to: (1) individuals could tolerate a higher cost imposed for the benefit of a relative than for that of a non-relative (and group members could be more closely related in small nests); and (2) prey usually captured in larger nests might be too large to allow some few individuals to monopolise it.

Because a small number of colonies were collected in each period, we did not test the relationship between nest size and spider size variations. In spite of this, some very large colonies, such as one collected in September, with 308 individuals, presented a coefficient of variation of spider carapace area lower than that of others from relatively smaller nests. On the other hand, some very small colonies, such as another one collected in September (with 17 spiders), presented an even lower CV value. Thus, additional samples must be taken in order to analyse the influence of nest size on A. jabaquara individuals’ size variability.
There are three possible explanations for the differences in weight gain between prey-size groups in the laboratory experiment. The first one is that spiders consumed the same amount of food from both prey types, but *Anastrepha* sp. represents a richer nutritional resource than *D. melanogaster*. We have no data to support or reject this explanation. Even if prey types have similar nutritional values, spiders could have extracted a higher proportion of weight from large flies. Rypstra (1990a) found that *A. eximius* extract food from large prey more efficiently than from small ones. In another experiment, however, she found similar values for fruit and houseflies (Rypstra, 1993). The third possibility is that spiders were always attracted by the large flies’ movements, while several small flies usually remained intact until death. Soon after death the nutritional value starts to decrease due to decomposition (approximately 70% weight loss after two days; M. Gonzaga, pers. obs.) and the available biomass reduces. Despite these possible differences, we found a significant increase in weight in both groups, suggesting that food supply was enough to prevent death and promote growth (we registered 18 exuvia in group 1 and 16 in group 2).

The solitary capture and consumption of small insects, reported here for *A. jabaquara*, has also been reported for *A. eximius* (Pasquet & Kraft, 1992; Ebert, 1998) and *A. studiosus* (Brach, 1977). A high proportion of the insects subdued in *A. eximius* webs, however, are larger than individual spiders (Nentwig, 1985; Rypstra, 1990b). Vollrath & Rodhe-Arndt (1983) attribute size variation within *A. eximius* colonies to competition over large patches of food. Rypstra (1993) also discusses the importance of competition in establishing social structure and hierarchical organisation in this species.

Although we previously observed that the initial weight of each individual was not an important factor for determining the time spent consuming prey items in small artificial *A. jabaquara* groups (Gonzaga & Vasconcellos-Neto, 2002), we registered a tendency of increase in spiders weight variation after a short period of being supplied only with medium-sized prey (*Anastrepha* sp.). This suggests that the benefits of group foraging in *A. jabaquara*
may be unequally distributed among colony members. Differences in food acquisition, however, seem to be not completely determined by contests over displaced prey parts or feeding positions (see Gonzaga & Vasconcellos-Neto, 2002). Thus, other factors, such as possible differences in capabilities of food extraction and metabolism, must also be considered as relevant sources of size variability among nestmates.

The especially high coefficient of variation in subgroup C was probably due to the decrease in group size and to the cannibalistic event(s). Schneider (1995) found that, for Stegodyphus lineatus, under laboratory conditions, the initial CV within groups was positively correlated with the probability of dying for the smallest spiders in the group. Despite similar initial variation in our subgroups, differences in spider size after the beginning of the experiment and the restricted space in recipients might have favoured cannibalism.

It is important to evaluate now (1) the frequency of contests in natural colonies and its influence on food partitioning; (2) if large spiders, independent of interactions with other individuals, remove more food than smaller colony members; and (3) the frequency of solitary captures and cannibalism in natural colonies.

References
